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THE REACTIONS OF PLANTS TO ULTRA-VIOLET

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GENERAL CONSIDERATIONS

It has been recognized for a considerable time that in general, as Ellis and Wells ('25) observe, there are two effects of ultra-violet radiations upon organisms, designated as stimulative and lethal, with the dividing line approximately at 2900 Å. If, however, various types of organisms and their different functions are considered separately both the exact significance of these terms and the limits of the regions concerned must be defined more explicitly. In addition, the numerous environmental factors so modify the effects of any one of them that unless the conditions are exactly stated there is a conflict of results such as has been emphasized by Popp and Brown ('33). It must be recognized, however, that such conflict of results is due to the different conditions under which the experiments have been carried on, the differences in physiologic action of various combinations of ultra-violet regions, and the specificity of organisms, rather than to a non-responsiveness of plants to ultra-violet.

The terms "stimulative" and "lethal" must be defined in relation to definite standards, and when we are dealing with a complex organism and especially with one of our higher plants which is not so completely integrated as are the higher animals, we must recognize that these terms may be applied either to the whole organism or to one or more of its parts or functions. As is well known, the lack of a proper amount of light results in the etiolation of green plants. Under such conditions the use of ultra-violet irradiation cannot be expected to give a stimulation which will reveal itself in greater elongation. In fact the opposite result, as might be expected from the known action of the violet end of the spectrum, actually occurs. Under conditions of reduced visual illumination tomato plants irradiated with the mercury arc are shorter than those which are unirradiated, although with a moderate amount of irradiation from the mercury arc the dry weight of tissue produced may be the same as in the somewhat etiolated, unirradiated plants (table I). More strongly irradiated plants under the same conditions develop less tissue as determined by its dry weight, and correlated with this reduced vegatative growth there may be much more abundant formation of green fruit.

TABLE I

REACTION OF TOMATO PLANTS TO ULTRA-VIOLET IRRADIATION UNDER REDUCED VISIBLE ILLUMINATION

	Set A*	Set B*	Set C*
Average increase in height in 2 months	28.9 cm.	21.6 cm.	20.9 cm.
Average dry weight	0.73 gm.	0.71 gm.	0.57 gm.
Weight of green fruit produced	(26 plants) 26.3 gms.	(26 plants) 23.1 gms.	(20 plants) 55.7 gms.

* Set A (30 plants) unirradiated controls. Set B (29 plants) and C (21 plants), irradiated at 50 inches from the mercury vapor arc through a water filter of Vita glass, 9 minutes and 18 minutes daily, respectively.

Thus it is evident that the action of ultra-violet on these plants may result at the same time in reduction of elongation and in an increase in fruit formation. On the other hand, a reduction in the amount of ultra-violet attained by increasing air absorption through greater distance, concurrent with a more normal amount of visible illumination as evidenced by lack of etiolation in checks, results in actual increase in dry weight, elongation, and mineral content (Fuller, '31). Similar results have been obtained in other series of experiments in our laboratory more recently and have also been reported by others (Benedict, '34), all of which indicate clearly that the criteria of "stimulation" and "injury" vary with the species and with the different conditions under which they are studied. We cannot determine at the present time how much of the effect is due to direct action and how much to indirect. Thus it is probable that the greater fruit formation in plants showing strongly retarded vegetative growth is due largely to the disturbed nutritional balances as may be inferred from the work of Kraus and Kraybill ('18), Murneek ('26), and Harvey ('31), yet some direct stimulation is possible. As will be demonstrated in later papers in this series, various phases of respirational activities react differently to the same ultra-violet regions. Enzymic activity may be stimulated as shown by Fuller ('32), v. Euler and Günther ('33), Bersin ('33), and from studies to be reported in a later paper in this series, and this may occur when there is coincident evidence of injury to other systems.

It is especially important therefore to examine the applications of our criteria in order to avoid much needless discussion of results based upon uncertainty in their use and to determine the conclusions which may properly be drawn. In the study of the effects of radiations upon organisms many indefinite factors exist, not the least of which is the variety of material used in the experiments. It is now well understood that while there are certain broad fundamental ways in which all green plants are similar in their physiology, yet each species and variety has a physiology of its own both qualitatively and quantitatively different from that of any other. We do not know as yet the experimental limits of this specificity in any given case except as expressed in the general results which give us the indistinct concept of the species. This one variable factor has given rise to many pages of useless discussion in the papers on radiations. To expect all plants to respond uniformly to such a complex environmental factor as ultra-violet is to ignore their specific character as well as the specific action of different types and quantities of energy.

Another general factor which frequently is forgotten is the historical, evolutionary development of the plant kingdom. The physical concept of a smooth cumulative curve of effects from a given kind of force, such as increasing heat causing an increasing expansion of an iron bar, has restricted value when applied to plants. They have been subjected through eons of time to circumscribed ranges or intensities of certain physical and chemical conditions to which they have become adjusted. Therefore in subjecting them experimentally to the entire range of a given force we should expect them to respond in one manner in the range to which they have become adjusted and in another manner in the ranges outside of their historical experience. Thus we find that within a certain restricted range of temperature most plants increase in size in a direct ratio to increased temperature, while outside of this range they react quite differently. It is necessary of course to take into consideration in such a statement a certain elastic adaptability which enables living organisms to extend their responses somewhat normally even beyond the usual range of the physical factors. These two variables, plant specificity and specific adjusted reaction to certain ranges of each environmental factor, are probably more important in influencing attempts to obtain generalizations than many other factors which have been so greatly stressed by some.

As concerns growth related to any external stimulus, there are evidently three possible general conditions: (1) it may be definitely increased over that under established standards due to dominance of stimulative over retarding influences; (2) it may be definitely reduced below the established standards, due to dominance of retarding factors over stimulative ones; and (3) there may be such a balance of these two sets of effects that no significant increase or decrease can take place. It is possible also that in this last case certain physiological activities which are not reflected in growth may be stimulated or retarded. From the above considerations it is clear that growth cannot be a complete index of stimulative or lethal reaction of plants.

In the field of radiations growth as a criterion of stimulation must be carefully defined. Size, wet weight, dry weight, and number of leaves must all be given careful consideration and balanced against one another, for no one of them can be used exclusively to indicate stimulation. In the phase of reproduction radiations are coming to be recognized as more and more important, and we expect that stimulation will be evidenced in the number, form, and size of the fruiting structures at times when vegetative features fail to give evidence of reaction. Occasionally the phrase "beneficial effects" (Popp and Brown, '33) is used more or less as synonymous with stimulation, but it is liable to have a subjective rather than an objective content, and a very careful assessing of the values of the various stimuli and of criteria must be made before it can have a quantitative value. Thus a stimulated growth may be beneficial under certain circumstances and stages of growth, but positively injurious at other times, while the reverse may also be true. Let us now consider some of the ways in which growth has been used as a criterion in radiation experiments on plants.

Experiments, such as those of Popp and Brown ('28), in which the early seedling stages have been used as a test for stimulation, can hardly be used as a proof against the concept of stimulation as applied to older plants. It is a well-known fact in general physiology that the physiology of the young organism is often quite different from that of the more mature individual. Moreover, the growth curve of an individual shows an exceedingly rapid rise during the early seedling stages, and it is doubtful whether at this time all stimulative factors could be expected to affect the rate of growth even if they could at a later, slower period. On the other hand, retarding and limiting factors may become especially effective during the period of normally active enlargement. Thus a small decrease in the water supply at such a time may have a much greater effect than at a later stage and hence have a greater antagonistic action toward the tendencies of reaction to stimulative factors.

It is entirely probable that one of the reasons why growth is so active during the early seedling stages is that there is stored away in the seed a maximum amount of all sorts of food substances, including the vitamines, stimulative to rapid growth. As a seedling matures it tends to exhaust the stored supplies, or distribute them throughout more and more tissues, or remove them from further utilization by combining them in more or less stable, permanent compounds unless renewed by favorable physiological processes. If, as may well be, the stimulative action of ultra-violet radiations is due to the manufacture in the plant of stimulative compounds, some of which may be stored in the seed, adequate to the maximum stimulation of the developing seedling, the stimulative action of ultra-violet would not become manifest until after the essential exhaustion of the seed reserves. For a similar reason, if plants are growing under daylight conditions in which ultra-violet adequate to maximum stimulation for a given set of conditions has been supplied naturally, then additional raying from an artificial source would not be evidenced in stimulation. Hence experiments performed in one season of the year may not be at all comparable with those at another season, and likewise experiments under different aerial conditions such as arise from varying quantities of smoke, moisture, cloudiness, etc., cannot be fairly compared, nor equal value attached to negative results as to positive ones.

As illustrating the seasonal effects upon ultra-violet the following may be cited: In summer about 1 per cent of solar radiation is in the ultra-violet and about .04 per cent in the region 290 mμ to 320 mμ. In winter the figures are .2 per cent total ultra-violet and .013 per cent in the region 290–320 mμ (Laurens, '33, p. 54). While these values were obtained for a different region than ours, comparisons of numerous other determinations indicate that these are fair approximations for many other regions.

It has been our common experience in this laboratory that even injury from irradiation by an unscreened mercury vapor arc is much more difficult to demonstrate on tomato plants which have developed during the summer months in the greenhouse than upon those developed during the winter months. Older plants in the summer are likewise less easily injured by ultra-violet than younger ones. Some of these differences may no doubt be attributed to certain anatomical changes which occur in plants when rayed with ultra-violet such as described by Eltinge ('28).

From the various considerations just discussed it is evident that experiments showing lack of stimulation under ultra-violet cannot be used to condemn positive results unless it is certain that the other environmental and biological conditions have been duplicated. If one compares the investigations reporting lack of stimulation with those most carefully controlled which report stimulation (Fuller, '31; Benedict, '34), it is evident that no careful attempt has been made in the former to duplicate the conditions under which stimulation has taken place. It should be pointed out here that there is a decided difference in the conditions of irradiation between those in which there is given a long-time or close exposure of seeds, seedlings, and more mature plants to artificial irradiation sources and those in which short-time or long-distance exposures are made. Short injurious ultra-violet waves are much more fully absorbed by air than are the longer ultra-violet, and in short-time exposures the variable of visible light is eliminated in a practical manner and the variable of infra-red is also greatly reduced. Although both of these variables have been stressed recently (Popp and Brown, '33), as seriously influencing conclusions concerning the ultra-violet stimulation, it should be noted that there is a great difference between adding a little more visible light and some extra heat to the environment of a plant well supplied with these factors and adding ultra-violet to an environment almost devoid of such a factor. Shirley ('29), for example, records that the rise in temperature due to the heat from his 1500-watt lamps at 24 inches distance was less than 0.5° C., while Fuller's lamp was at 100 inches and a large electric fan was constantly used during irradiation to remove so far as possible any excess heating.

Since for all of the experiments reported from our laboratories the plants were grown in the winter or spring in the greenhouses, and much of the ultra-violet which is accepted as stimulative in character is screened out by greenhouse glass and reduced by climatic and seasonal conditions, it is evident that the plants would be in a condition to be stimulated by the ultra-violet from an artificial source. Such actual increased growth has been recorded in our laboratories for a variety of plants irradiated by a mercury vapor arc. Such distances and such screens were used as would remove injurious ultra-violet, and essentially eliminate the variables of added visible light and of infra-red since they constituted but a minute fraction, an average of nine minutes a day exposure, of the total of such energy received by the plants during the experimental growth period. In these experiments (Fuller, '31) where there were ten sets of one hundred plants each, both the wet weight and dry weight of all the sets rayed through filters which cut off the injurious ultra-violet were significantly greater than those of the unrayed controls. In six out of the eight rayed sets also significant increases in height occurred.

The pertinent question may be raised as to how one may explain the stimulative action of small amounts of ultra-violet on organisms when we are inclined to discount the larger amounts of visible and infra-red radiations from the same artificial source. It is rather generally accepted that within certain limits growth increases quantitatively with light and heat. On the other hand, the changes in plants caused by ultra-violet seem to be qualitatively different from those caused by other radiations (Jacobi, '28) and certainly cannot be estimated in terms of the quantity of energy available in the ultra-violet compared with that present in visible and infra-red radiations. Or we may say that a small quantity of energy added experimentally is more effective in this range of radiations than in the others, due perhaps to a more complete absorption and to the fact that the amount of ultra-violet added is proportionately very large during winter and early spring. Whether, as has been suggested (Laurens, '33), these shorter wave lengths cause special intimate molecular or atomic rearrangements we cannot at present know. It may be also that something akin to the rigor or tetanus produced in organisms by consecutive applications of stimuli might prevent stimulation in the presence of larger amounts of the same forces, but in the absence of natural ultra-violet of certain wave lengths an artificial application might be especially effective, particularly when added in successive, short doses. Johnston ('32) has recently used infra-red radiations in conjunction with light and found that when the latter was well below the optimum for tomato plants the near infra-red stimulated growth, but with a higher degree of illumination the infra-red stimulation was much less. This seems to indicate that stimulative action of the infra-red is much less effective as normal illumination is approached.

In conclusion we may summarize the discussion as follows: Physiological response includes both increased and decreased activities. Growth is a resultant of numerous physical and chemical reactions. Stimulation or increased growth may therefore be a resultant of some increases and some decreases of physical and chemical activities. Injury and retarded growth may indicate either a total resultant reaction of all the physical and chemical reactions or interference with some one or several specific reactions. Ultra-violet and X-radiations cannot be expected to affect every one of the numerous physical and chemical activities in an accelerative fashion or, on the other hand, all in a retarding fashion. Evidences are found all through the numerous studies on radiations to substantiate these statements. It is to be expected, therefore, that there will be numerous apparently contradictory results as long as growth alone is taken as a criterion for stimulation and interpreted as the result of purely quantitative applications of energy. This is especially true if the results from studies upon different species and varieties are massed together and compared. It is evident therefore that experimental studies which have failed to produce acceleration of growth cannot be used to impugn those which have demonstrated stimulation.

The element of critical surprise evidenced in Popp and Brown's ('33) summary of ultra-violet work, that such contradictory results are published, and the implication of untrustworthy data are not wholly justifiable in view of the considerations discussed above. We should expect just such a condition, and instead of attempting at the present time to amalgamate all such work into a consistent unit and to evaluate it in terms of uniformity of growth results, it would be more profitable to recognize the existence of numerous separate problems and allocate to each the data properly belonging to it. In some of the earlier work where only a reconnaissance of the field has been attempted conditions have not been completely controlled, and it is indeed true that in other studies unjustifiable deductions have been made, or poor technique has made the work essentially valueless as soon as more carefully controlled experiments are reported. Finally, the historical development of the plant kingdom has led to adjustments of plants to restricted ranges of environmental factors. Within these ranges any green plant will react quite differently than it will outside of them, and therefore even opposite reactions may be expected from the same plant in these different ranges, as, for example, stimulated growth in some radiations and retarded in others.

A series of investigations has therefore been initiated and is in progress in which separate physiological activities are being studied in relation to ultra-violet, in an effort to define the conditions under which stimulative and lethal actions occur.

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